

Projecting the recovery of a long-lived deep-sea coral species after the Deepwater Horizon oil spill using state-structured models

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Abstract

1. Deepwater coral communities are hotspots of diversity and biomass. Most deep-sea coral species are long-lived and slow-growing and are, thus, expected to recover slowly after disturbance. A better understanding of the recovery potential of these organisms is necessary to make appropriate management decisions.
2. We used data from high-resolution monitoring of individual coral colonies that were impacted by the Deepwater Horizon oil spill (April 2010) to parameterize and validate an annual, impact-dependent, state-structured matrix model to estimate the time to recovery for each coral colony. We projected the dynamics of three branch states: visibly healthy, unhealthy and hydroid-colonized. Although we implicitly included branch loss in the model, we focused on the short-term return of extant, damaged branches to a visibly healthy state and did not consider the far longer term regrowth of lost branches.
3. Our model estimates that, depending on the initial level of impact, corals impacted by the spill will take up to three decades to recover to a state where all remaining branches appear healthy, though the majority of corals are projected to reach that state within a decade. By that time, some of these colonies will have lost a significant number of branches, leading to approximately 10% reduction in total biomass at all impacted sites.
4. Overall, our model overestimates recovery, but branch loss estimates were reliable. Thus, the available growth rate data suggest that hundreds of years may be necessary for impacted communities to grow back to their initial biomass.
5. *Policy implications.* Our study quantifies the very slow recovery rate of deep-sea corals impacted by the Deepwater Horizon oil spill and demonstrates the imperative of prioritizing a precautionary approach for deep-sea ecosystems over restoration after the fact. As anthropogenic pressure on the deep sea is likely to increase, we suggest the establishment of coral monitoring sites implemented as part of Marine Protected Areas to limit and detect impact to deep-sea corals. Furthermore, our model may be used to plan shorter- and longer-term monitoring programmes after impact and to provide a timeline for policy.

KEYWORDS

anthropogenic impact, deep-sea corals, Gulf of Mexico, imagery, matrix models, monitoring programme, *Paramuricea biscaya*, resilience

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1 | INTRODUCTION

The blowout of the Deepwater Horizon drilling platform on 20 April 2010 in the Northern Gulf of Mexico led to the largest accidental oil spill in history. Approximately 4.9 million barrels (780 million litres) of crude oil were released over an 87-day period, before the well was capped in July 2010. In response to the spill, 7 million litres of dispersant were applied, with three million litres applied at depth, directly at the wellhead (McNutt et al., 2011). The Deepwater Horizon oil spill was unprecedented, not only because of its volume and duration, but also because the oil was released directly into the deep sea, at a depth of 1,520 m (Peterson et al., 2012). The deepwater plume, that persisted for several months at a depth of about 1,100 m (Camilli et al., 2010), as well as a large marine snow formation event in oil-contaminated surface water (Passow, Ziervogel, Asper, & Diercks, 2012), had the potential to impact numerous, poorly known, deep-sea communities.

In November 2010, a few months after the well was capped, an impacted deep-sea octocoral community was discovered (White et al., 2012). This community was located in Mississippi Canyon (MC) 294 (all site names are based on the US Bureau of Ocean Energy Management lease block designation for 3 × 3 nautical mile square areas of the sea floor leased for oil and gas activities), 13 km away from the well at a depth of 1,370 m. The majority of the corals at this site exhibited signs of impact; they were covered in a brown flocculent material (floc) which contained traces of oil from the Macondo well, as well as dioctyl sodium sulfosuccinate, a surfactant used in the dispersant Corexit applied in the aftermath of the spill (White et al., 2012, 2014). In 2011, two more impacted coral communities were discovered at MC 297 and MC 344 located 6 and 22 km away from the well at 1,560 and 1,850 m depth, respectively (Fisher et al., 2014). Coral colonies were not covered in floc but displayed the very characteristic pattern of spatially patchy impact and hydroid colonization across the colony observed on corals from MC 294 at the same time, after the floc had disappeared.

Deepwater corals are found at all latitudes in the deep sea (Watling, France, Pante, & Simpson, 2011) and are used by numerous species as habitat, feeding grounds, or nurseries (Baillon, Hamel, Wareham, & Mercier, 2012; Buhl-Mortensen, 2004; Du Preez & Tunnicliffe, 2011; Etnoyer & Warrenchuk, 2007). In addition to enhancing biodiversity, cold-water corals have been shown to play a role in carbon cycling (Cathalot et al., 2015; Oevelen et al., 2009). Corals from the octocorallia subclass, although not reef-forming, can occur in very dense assemblages, and provide structurally complex habitats that can also support a high diversity of organisms (Buhl-Mortensen & Mortensen, 2004, 2005; Buhl-Mortensen et al., 2010; Roberts, Wheeler, & Freiwald, 2006).

Given their important role in structuring deep-sea communities, a fuller understanding of how these corals will recover from acute damage, in general, and the Deepwater Horizon spill, in particular, is essential. Recovery comprises two main processes in this coral system: the observable recovery of extant, but damaged, biomass to a healthy state and the replacement of lost biomass (specifically,

regrowth of lost branches). Recovery processes are complex and dependent on numerous factors (Henry & Hart, 2005). Regeneration from injuries can depend on the size, age, genotype or morphology of the corals, as well as external factors, such as the environment, and the presence of predators, competition (Henry & Hart, 2005; Lasker, 1990; Linares et al., 2005; Meesters, Noordeloos, & Bak, 1994; Meesters, Wesseling, & Bak, 1996).

Many deepwater coral species have very low metabolic and growth rates and are extremely long lived (Andrews et al., 2002; Roark, Guilderson, Dunbar, Fallon, & Mucciarone, 2009). In the Northern Gulf of Mexico, some *Paramuricea biscaya* (Grasshoff, 1977) colonies, the octocoral species that was most affected by the spill, have been estimated to be over 600 years old (Prouty, Fisher, Demopoulos, & Druffel, 2014). The low metabolic and growth rates of these corals suggest that it could take many years before even moderately impacted colonies completely recover (in terms of both return to health of extant branches and regrowth of lost branches) from the impacts of the spill.

A slow and complex recovery of corals impacted by the Deepwater Horizon oil spill has already been suggested by several studies. Two years after the Deepwater Horizon oil spill, even though the median level of visible impact at MC 294 had decreased, most impacted *P. biscaya* still showed signs of injury, and hydroid overgrowth, which started in 2011, was still expanding on some colonies (Hsing et al., 2013). Hydroids colonized damaged portions of the colonies, impeding tissue regeneration and weakening the coral's skeleton due to the added epibiont mass (Bavestrello, Cerrano, Zanzi, & Cattaneo-Vietti, 1997). Branch loss was observed on some colonies, and the recovery of individual damaged branches and branches colonized by hydroids was negatively correlated with the initial level of impact to the colony. The recovery patterns of impacted coral colonies also varied with the presence or absence of the brittle star (ophiuroid) *Asteroschema clavigerum* (Verrill, 1894) on the corals. *A. clavigerum* ophiuroids both provided protection from impact and facilitated recovery of damaged coral branches (Girard, Fu, & Fisher, 2016).

Long-term monitoring of impacted coral colonies is the best way to study the recovery of these long-lived, slow-growing organisms. However, collecting data in the deep sea is challenging and expensive, and expectations are that it will take decades to centuries for full regrowth and recovery of these coral communities. Thus, we, here, specifically focused on how long it will take for observable recovery to health of extant coral biomass. Estimates of time to visible recovery will allow for the appropriate planning of both the overall duration of a recovery monitoring plan, and also of the frequency of visits necessary for recovery assessment. After extant coral recovery, less frequent monitoring may subsequently document the slower regrowth process, which was not addressed in the present study. For our study, we used a structured matrix model (Caswell, 2001) to estimate how long it will take for the impacted corals to visibly recover from damage and hydroid colonization, and thus for how long monitoring will be informative about the health of remaining coral biomass.

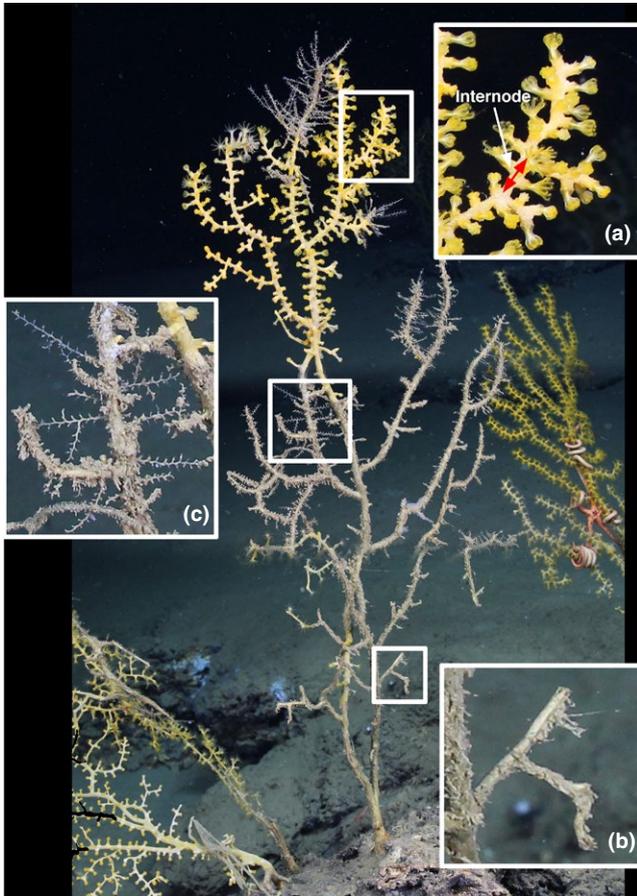


FIGURE 1 Impacted coral colony from MC 294. The three branch/internode states are visible: a few branches are visibly healthy (a), but the majority are either unhealthy (b) or colonized by hydroids (c)

2 | MATERIALS AND METHODS

2.1 | Study sites and data acquisition

The data used for this model were collected as part of a long-term monitoring study at three sites that were impacted by the Deepwater Horizon oil spill. These sites, in BOEM lease blocks MC 294, MC 297 and MC 344, were located 13, 6 and 22 km away from the Macondo well, respectively, and the dominant coral species at these sites was *P. biscaya*. Corals from this species have a planar morphology; all branches are in the same plane and are, thus, visible in the same photograph, making them well suited for image analysis (Figure 1).

We monitored 49, 56 and 61 individual coral colonies between 2011 and 2017 at MC 294, MC 297 and MC 344, respectively. High-definition images of the same colonies were taken every year using digital still cameras and remotely operated vehicles (ROVs). A particular effort was made to use the same headings (compass bearings) and camera-object distance each time to facilitate comparisons. We chose to use images collected in October 2011 as the baseline for this study because this was the first complete, high-quality, dataset collected from all three sites, and the oil containing floc had fallen off the corals by this time, revealing the presence or absence of visible

damage. We digitized images from the 2011 cruise using Inkscape 0.48.5, and coded coral branches as visibly healthy, unhealthy (obvious tissue damage, bare skeleton or excess mucous production) or colonized by hydroids (Figure 1). We coded branches conservatively; whenever it was not clear whether a branch was impacted, we coded it as healthy, and when the presence of hydroids was not obvious, we coded the branch as unhealthy. To determine the condition of coral colonies after 2011, we used the 2011 image as a template and re-coded branches every year based on their new state. After 2011, we added a new category for branch loss. We followed changes from one state category to another on individual branches between consecutive years using the digitized high-definition images. We counted the total number of branches on each coral colony using the cell counter tool in ImageJ 1.4 and measured the proportion of branches that were in each state for every year. We then tracked changes in individual branches and measured the proportion of branches that changed from one state to another, or not, between consecutive years.

In addition to quantifying impact for each coral colony, we estimated total branch length for each coral. To estimate the size of each colony, a perforated resilient plastic ball ("wiffle ball"), with a diameter of 8.9 cm, mounted on a pole was held next to each coral colony and imaged with the colony to provide scale. For these measurements, the mounted ball was held in the manipulator of the ROV, in contact with the colony, and imaged in the same plane. We then used these images to calculate the total branch length of each coral (cumulative length of all branches). We used total branch length as a measure of coral size and a proxy for biomass.

2.2 | Model

We projected the level of total visible impact for each coral colony using an annual impact-dependent state-structured matrix model (Caswell, 2001) where three states were considered: branches could either be healthy, unhealthy or colonized by hydroids (Figure 1). In this model, internodes (distance between the base of two branches; Figure 1a) used here as a proxy for branches, constituted individuals. The number of branches in each category at time $t + 1$ was given by the linear equation:

$$\mathbf{n}(t + 1) = \mathbf{U}\mathbf{n}(t)$$

where $\mathbf{n}(t)$ is a vector representing the number of branches in each state, and \mathbf{U} is the projection matrix, containing the transition probabilities between each of the three states (see Appendix S1 for the full-model structure).

The transition probabilities were dependent on the level of total visible impact of the colony (sum of the proportion of unhealthy and hydroid-colonized branches) each year, thus the projection matrix changed at every model time step, making the model impact-dependent. In this model, the sum of the transition probabilities for each state was less than or equal to one; probabilities less than one denote branch loss. Regrowth of new, healthy, branches was explicitly excluded from this model as we focused on the recovery to

health of extant coral biomass, and growth rates for this coral species are extremely slow (Prouty et al., 2014).

We assumed that all coral colonies responded the same way to impact and that the transition probabilities only depended on the current state of the system, as is common in matrix modelling (Caswell, 2001). The number of branches in each state in 2011 was used as the initial condition as, in 2010, fewer corals were imaged at MC 294, and none were imaged at MC 297 or MC 344.

2.3 | Parameter estimation

We estimated the transition probabilities for the projection matrix with generalized linear mixed models (GLMMs). As changes in the state of individual branches depended on the overall level of impact and size of the colonies, we used the total visible impact proportion (IMP), and total branch length in 2011 (SIZE)—both continuous variables—for each coral as fixed effects in the statistical model. Since we imaged the same coral colonies every year, we treated year (YEAR) as a random effect. We also included coral colony (CORAL) as a random effect to avoid overdispersion (when the variability in the data is larger than the variability expected under the assumed distribution [binomial in the case of proportion data], leading to poor model fitting). As an alternative to multinomial models (which could not accommodate our random effects), we used the same 3-step sequence of nested binomial GLMMs (Caswell, 2001, p. 55; Shea & Kelly, 1998) for each branch state (healthy, unhealthy, or hydroid-colonized). At each step, we used a logit link function to estimate the effect of impact proportion and size on the proportion of branches that changed from one state to another:

1. We first modelled the proportion of branches that broke. The response variable for this model consisted of two columns: one for the number of branches that broke and the other for the number of branches that did not break (which sum to the total number of branches in the focal state).

2. We then modelled the proportion of branches that stayed in the same state between consecutive years, considering only branches that did not break.
3. Finally, we tested the effect of impact and size on the proportion of branches that transitioned to either of the remaining two states, considering only branches that did not break and did not remain in the same state.

Each step was, thus, performed on nested subsets of the data, starting with the relevant subset (for instance, only healthy branches were used when modelling the transition from healthy to any other state). For each transition probability, we started with the same full model:

$$\text{Transition probability} \sim \text{IMP} + \text{SIZE} + \text{IMP} \times \text{SIZE} + (1|\text{YEAR}) \\ + (1|\text{CORAL})$$

and selected the minimum adequate model (Table 1).

The marginal estimates from the minimum adequate model were then used to predict the transition probabilities used in the matrix model for all coral colonies. When impact proportion or size did not have a significant effect on a particular transition, the weighted mean for this proportion was used to estimate the transition probability.

We tested models parameterized using all possible combination of years (the effect of different years on model outcomes was inconsistent and rarely significant; see Appendix S2). We then used the data from 2011 to 2015 at MC 294 for model parameterization because corals at this site displayed the largest range of impact levels, and impact at this site was directly linked to the Deepwater Horizon oil spill (traces of oil and dispersant were detected in the deposit that covered coral branches). Although the impact distribution indicates that corals at MC 297 and MC 344 were also impacted by the oil spill, the extent of impact in 2010 is unknown for these corals as they were only discovered in 2011. Corals at MC 294, as well as MC 297 and MC 344, were then used to validate model projections, in order to determine whether the estimates based on the MC 294 corals could be generalized to other sites.

TABLE 1 Parameters selected for each transition probability and associated model coefficients based on the generalized linear mixed models

Transition	Model	Intercept		IMP		SIZE	
		Estimate	SE	Estimate	SE	Estimate	SE
H→B	0.0067						
H→H	~IMP	5.45	0.194	-4.10	0.523		
H→I	0.811						
I→B	0.0989						
I→I	~IMP	-1.23	0.384	1.79	0.444		
I→H	~IMP	2.42	0.431	-4.90	0.708		
Hy→B	0.122						
Hy→Hy	~IMP	-0.671	0.389	1.82	0.699		
Hy→H	~IMP + SIZE	0.425	0.570	-3.81	0.517	0.145	0.0591

IMP, total visible impact (unhealthy and hydroid-colonized branches); SIZE, total branch length; H, healthy branches; I, unhealthy branches; Hy, branches colonized by hydroids; B, branches that broke. Random factors: Imaging year and individual colony number.

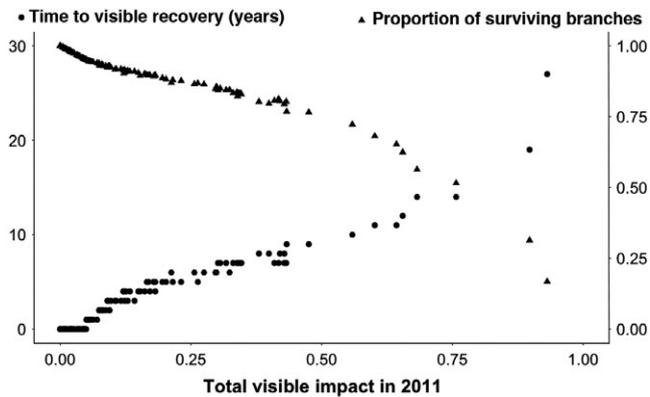


FIGURE 2 Estimated time to visible recovery and proportion of surviving branches for all corals at MC 294, MC 297 and MC 344 as a function of total visible impact (unhealthy and hydroid-colonized branches) in 2011

2.4 | Model validation

For each coral colony at MC 294, MC 297 and MC 344, we projected the proportion of branches in each state in 2016 and 2017 and plotted it against the observed proportions for the same years. We then fitted linear regression models to assess the adequacy of model projections. For this analysis, we only included 91 corals (33, 41 and 17 at MC 294, MC 297 and MC 344, respectively) that were imaged every year between 2011 and 2017.

2.5 | Recovery estimation

We estimated the time to visible recovery (95% of the remaining, extant colony is visibly healthy) for every impacted coral colony at MC 294, MC 297 and MC 344 (38, 49 and 38 corals at MC 294, MC 297 and MC 344, respectively). Our model never projected 100% visible recovery, instead a steady state was reached between healthy, unhealthy and hydroid-colonized branches, with the proportion of healthy branches always being approximately 0.95. Since corals lost branches over time, we also estimated how much of the initial colony still existed after visible recovery (proportion of surviving branches). To evaluate the effect of the initial level of impact on the time to visible recovery and proportion of surviving branches, we ran deterministic simulations over a 50-year period using all possible combinations of the proportions of unhealthy and hydroid-colonized branches as initial conditions (we used a step size of 0.01 to discretize these variables). We used the average number of branches (170 [SD 150.5]) and total branch length (3.11 m) measured in 2011 at MC 294, MC 297 and MC 344 for all simulations.

2.6 | Elasticity analysis

We conducted an elasticity analysis by looking at the effect of a 0.1% decrease in each transition probability (separately) on the time to visible recovery, and comparing the difference between the

respective estimated times to visible recovery projected for all possible values of damage and hydroid colonization proportions (step size of 0.01) using deterministic simulations over a 50-year period.

All analyses were performed in R (R Core Team, 2014). GLMMs were fitted with the *lme4* (version 1.1-12) R package (Bates, Maechler, Bolker, & Walker, 2015), while the model was coded using the *popbio* (version 2.4.3) package (Stubben & Milligan, 2007).

3 | RESULTS

The level of total visible impact significantly affected all transition probabilities except for the transition from a healthy to an unhealthy state (Table 1). Coral size only had a significant effect on the transition from hydroid colonization to healthy. Neither impact nor size had a significant effect on the proportion of branches of any state that broke between consecutive years.

The time to visible recovery and proportion of surviving branches after visible recovery were estimated for 38, 49 and 38 coral colonies at MC 294, MC 297 and MC 344, respectively. These corals covered the full possible range of total visible impact, with the majority of colonies being lightly impacted (less than 20% impacted) and a few colonies having a level of impact close to 100%. The model projected that, although it will take up to 27 years for the most impacted coral colonies to visibly recover, the majority of coral colonies will have recovered within 10 years (Figure 2). The average and median times to recovery were both equal to 5 years (SD 4 years). The most heavily impacted coral colonies were found at MC 294, and corals, here, were projected to take 7 years (SD 6 years; median 4 years) on average to recover. An average of 5 years (SD 3 years) will be necessary for corals to visibly recover at both MC 297 and MC 344, with some colonies needing up to 12 years (median 5 years) at MC 297, and 11 years (median 7 years) at MC 344 to visibly recover.

The most impacted colonies were projected to lose more branches, and as a consequence, to have a lower proportion of surviving branches (Figure 2). For example, the most impacted coral colony included in this study was observed at MC 294 and over 90% of the colony was impacted in 2011. The model projected that this particular colony will look healthy by 2038, but, by that time, only 17% of the initial colony will remain. On average, 81% (SD 20%; median 89%), 88% (SD 7%; median 89%) and 86% (SD 8%; median 84%) of branches at MC 294, MC 297 and MC 344 were projected to remain after visible recovery.

Based on model simulations, we estimated that it could take up to 28 years for an impacted coral colony to recover to the point that approximately 95% of the colony is visibly healthy, depending on its initial level of impact (Figure 3a). The higher the initial proportion of unhealthy or hydroid-colonized branches, the longer it will take for a colony to recover. Moreover, for the same proportion of unhealthy and hydroid-colonized branches, the time to visible recovery was slightly longer when branches were colonized by hydroids (Figure 3a).

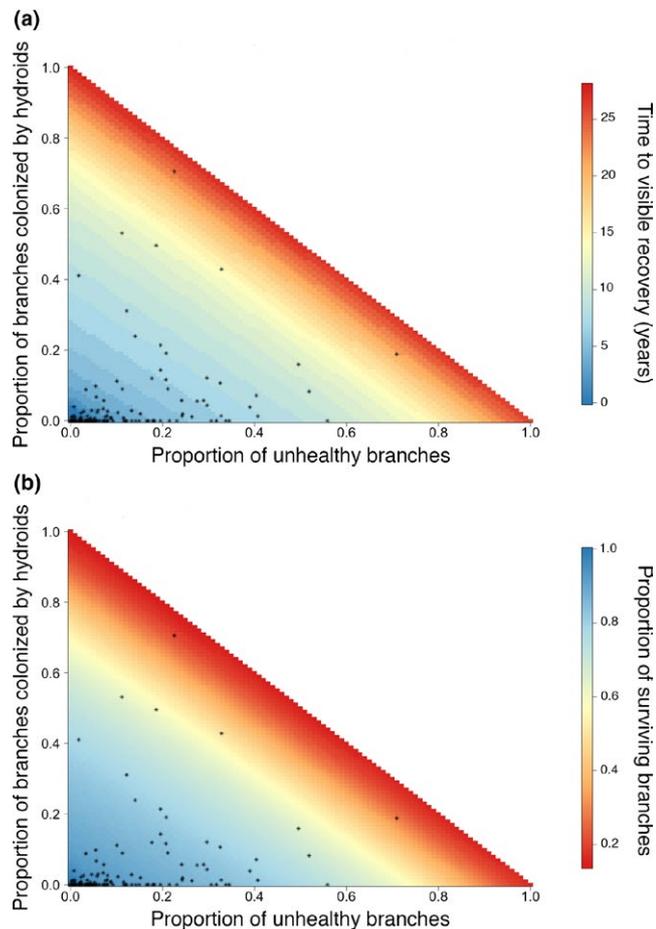


FIGURE 3 Time to visible recovery (a) and proportion of surviving branches (b) estimated by the model for different proportions of unhealthy and hydroid-colonized branches. Projections were based on deterministic simulations run for a period of 50 years. Only the proportion of branches in each of the three states varied; all other parameters were fixed as described in the Methods. The black stars represent the initial proportion values of the corals observed at all three impacted sites (MC 294, MC 297 and MC 344)

The proportion of surviving branches after a colony visibly recovered was also dependent on the initial level of total visible impact (Figure 3b). It varied between 0.99 for colonies that were initially lightly impacted and 0.14 for heavily impacted colonies. This effect was also slightly more pronounced for hydroid-colonized compared with unhealthy branches.

The time to visible recovery was the most sensitive to a decrease in the probability of a healthy branch remaining healthy, with a 0.1% decrease in this probability delaying visible recovery by 1 year (Appendix S3). Similar decreases in all the other transition probabilities had no detectable effect on the time to visible recovery (the few instances where an effect appears are due to the results not being completely smooth as they were based on numerical simulations).

After summing the total branch length of all impacted coral colonies at both sites, we found a total length of 141 m at MC 294, 136 m at MC 297, and 59 m at MC 344 in 2011. By the time all coral colonies at these sites were projected to have visibly recovered (after 27 years at MC 294, 12 years at MC 297 and 11 years at MC 344),

the projected total branch lengths were 121, 124 and 57 m, indicating an expected 14%, 9% and 3% reduction in total biomass at MC 294, MC 297 and MC 344, respectively.

Overall, the model tended to overestimate recovery. The projected proportions of healthy branches were higher than the proportions observed in 2016 and 2017 for most corals at all impacted sites (Figure 4). Conversely, the projected proportions of unhealthy and hydroid-colonized branches were significantly lower than the observed proportions in both 2016 and 2017. Branch loss projections were more reliable but still underestimated (Figure 4). The same trends were observed in both 2016 and 2017, and projection accuracy was the same for MC 294 (used for parameterization) as for MC 297 and MC 344, which were not included in model parameterization.

4 | DISCUSSION

At least 81 coral colonies were clearly impacted by the 2010 Deepwater Horizon oil spill at MC 294, MC 297 and MC 344, and our model projected that, even though most coral colonies will have visibly recovered within a decade, it will take up to ~27 years for some of these corals to visibly recover.

We estimated approximately a 3%–14% reduction in total biomass at our field sites by the time all corals appear to have recovered. Similar trends were observed with *Paramuricea clavata* after a mass mortality event in the Mediterranean Sea where, in some places, 70% of the biomass was lost (Cerrano et al., 2005; Linares et al., 2005). Due to the slow growth rates observed for these deep-sea corals in the Gulf of Mexico (Prouty et al., 2014), it will likely take hundreds of years before these coral communities grow back to their original biomass. Moreover, in addition to growing slowly, these corals also have low recruitment rates (Doughty, Quattrini, & Cordes, 2014; Linares, Coma, Garrabou, Díaz, & Zabala, 2008). As a result, the recovery of the impacted coral communities depends strongly on the ability of individual coral colonies to recover from damage. Importantly, recovery depends on the ability of coral colonies to remain healthy as suggested by the higher sensitivity of time to visible recovery to the probability of a healthy branch remaining healthy (likely due to the fact that the healthy to healthy transition probability was the largest).

Our results provide further evidence for the low resilience of deep-sea corals to disturbance, and the fragility of cold-water coral ecosystems. With new advances in technology and increases in human population, the number of threats to deep-sea ecosystems increases. A large body of literature shows that fishing activities, and especially bottom trawling, are major threats to deepwater coral communities (Clark & Koslow, 2008; Clark et al., 2010; Hall-Spencer, Allain, & Fossà, 2002; Koslow et al., 2001). Even though the impact of oil extraction and future mining activities is not as well characterized, there is a growing concern that the direct physical disturbance and sediment plumes produced by these activities may be as detrimental as trawling (Clark et al., 2010; Cordes et al., 2016; Van Dover, 2007).

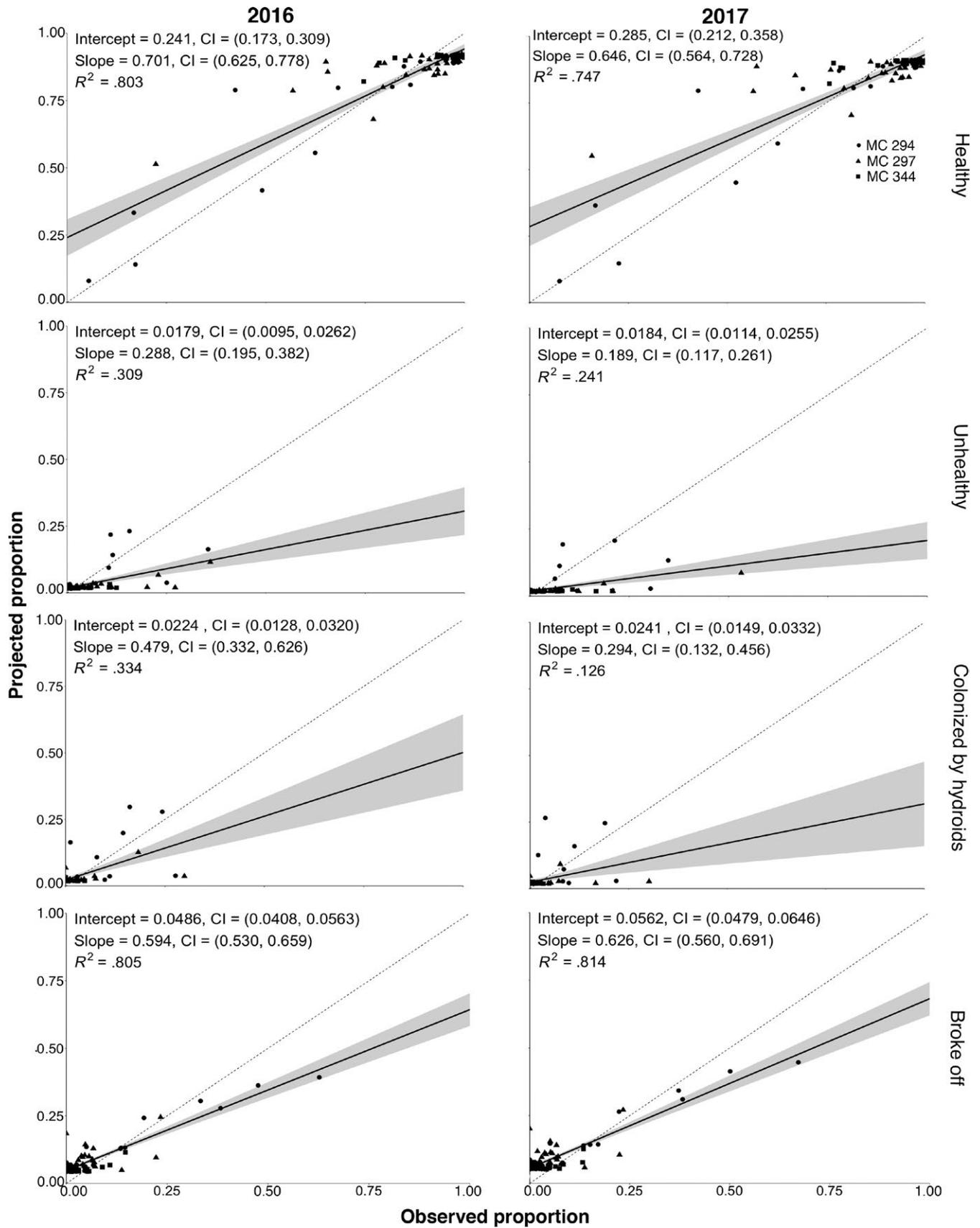


FIGURE 4 Comparison between the observed and projected proportion of branches in the three different states (healthy, unhealthy and hydroid-colonized) in 2016 and 2017 and of branches that broke between 2011 and 2016/2017. Linear regression models were fitted to the data. The slope, intercept, R^2 value and their corresponding 95% confidence intervals are indicated

To limit the impacts of human activities on deep-sea coral communities, an increasing number of fisheries closures, Marine Protected Areas and Special Areas of Conservation have been designated. However, so far only a few studies have assessed the effectiveness of these conservation measures. A follow-up study assessing recovery at the Darwin Mounds, after their closure from bottom trawling in 2003, found that protection was successful in maintaining live coral cover, but that areas that were heavily fished prior to closure showed no signs of recovery by 2011 (Huvenne, Bett, Masson, Le Bas, & Wheeler, 2016). These results emphasize that prevention of anthropogenic impact is essential for the conservation of deep-sea ecosystems.

While branch loss estimates for both 2016 and 2017 were reliable, our model underestimated the proportion of impacted (unhealthy or hydroid-colonized) branches. It is possible that the factors we considered in this model were not sufficient to fully explain recovery. One factor that we did not include in our model, but that may have played an important role in recovery, is the size of individual lesions (damaged areas). Preliminary exploration of our dataset showed that lesion size was significantly negatively correlated with the recovery of both unhealthy and hydroid-colonized branches. Moreover, the coral colonies for which the impact projections were the poorest were the corals that had the largest lesions. Similar effects of lesion size on regeneration have been observed for other coral species (Lirman, 2000; Meesters, Pauchli, & Bak, 1997).

In this study, we parameterized our model based on visible impact and did not take potential subacute effects into consideration. Crude oil has been shown to physiologically affect several fish species (Incardona et al., 2014), and toxicity experiments on different octocoral species indicated that mixtures of oil and dispersant were particularly toxic to corals (DeLeo, Ruiz-Ramos, Baums, & Cordes, 2015; Frometa, DeLorenzo, Pisarski, & Etnoyer, 2017). In addition to direct contact with oil and/or dispersant, corals could have ingested contaminated marine snow or zooplankton, potentially affecting their viability in the longer term (Mitra et al., 2012; Passow, 2014). It is, thus, possible that our model overestimated coral recovery because it did not include potential non-acute, long-term impact.

Finally, we modelled branch dynamics, and branches were treated as independent units. Matrix models assume that individuals are independent and that the survival of a specific individual has no impact on the fates of other individuals (Caswell, 2001). Corals are colonial, modular organisms, they are formed of replicated modules (polyps) that are capable of all physiological functions but are interconnected and genetically identical. Therefore, branches, which constitute individuals in our model, are not completely independent, and violating the assumption of independence may have affected the accuracy of our model projections. Cases where this assumption is violated generally require more complex models (Caswell, 2001), but we had insufficient data to develop such models. However, the non-independence of individuals likely had a limited effect on our model projections due to the fact that we modelled branch loss (the main source of non-independence since branch loss depended mostly on the location

of breakage rather than the state of the branches that were lost) first when parameterizing the model, and thus, branch loss did not directly influence the estimation of transition probabilities between the different states.

Another consequence of branches being interconnected is that a change in one part of a coral colony will be likely to affect the rest of the colony (Sánchez & Lasker, 2003). For instance, the observed effect of the total initial impact to *P. biscaya* colonies on the recovery of individual branches after the Deepwater Horizon oil spill indicated that damage to one part of the colony influenced the recovery of other parts of the colony (Hsing et al., 2013). Other studies have shown that, although the presence of surrounding healthy tissue was important for the regeneration of small lesions, colony integration and energy re-allocation play an important role in recovery (Oren, Benayahu, Lubinevsky, & Loya, 2001). We used an impact-dependent model to include the effect of total visible impact on the recovery of individual branches but, for a future study, this colony level integration could be better accounted for by using more sophisticated models.

Our model suggests that corals that were the most impacted by the Deepwater Horizon oil spill could take up to three decades before the remaining branches visibly recover, and that visible recovery of individual colonies is dependent on their initial level of impact. However, the bulk of the recovery is expected on timescales on the order of a decade. There was no difference in the accuracy of model projections between sites that were used (MC 294) or not (MC 297 and MC 344) to parameterize the model, suggesting that our results can be generalized to other coral communities dominated by *P. biscaya* in the Northern Gulf of Mexico. We here studied corals impacted by an oil spill, but our approach could be used to design monitoring projects following any type of anthropogenic impact on deep-sea octocorals. Specifically, our modelling approach can be used to evaluate the duration and frequency of a monitoring programme needed to document recovery based on different initial impact levels. In the case of the communities impacted by the Deepwater Horizon oil spill, annual monitoring for a decade following the spill, which would allow researchers to both document recovery and collect additional data to revise and improve the model, would be ideal. However, considering the high costs associated with doing research in the deep sea, we suggest continued monitoring every 2 years for a decade instead; this is sufficiently frequent to characterize coral recovery (changes in coral health are slow), though it provides fewer data for the model. Subsequently, lower frequency monitoring for a further two decades would be necessary to assess non-acute effects and to follow the potential recovery of the most heavily impacted colonies.

The significant branch loss observed and estimated indicates that hundreds of years will be necessary for both individual corals and the communities to grow back to their original size, and hence for the associated deep-sea communities to fully recover. Further, the considerable loss in coral biomass at each of the impacted sites was estimated without including any of the colonies killed initially, or damaged coral colonies that were collected as part of the Natural

Resource Damage Assessment Program. Overall, our results highlight the urgent need to better understand the biology of these organisms, and future modelling work could then include additional factors that might influence recovery. The low resilience of these deep-sea corals supports the need to limit impact to these extremely vulnerable ecosystems, rather than rely on restoration to bring communities back after impact. Marine Protected Areas implemented in association with photo-based monitoring would have the potential to both limit anthropogenic impact to deep-sea corals and detect changes in the health of corals resulting from mechanical, chemical, or thermal insults.

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AUTHORS' CONTRIBUTIONS

C.R.F. designed the study. F.G. and K.S. conceived the model and designed methodology; F.G. collected the data; F.G. analysed the data; F.G. led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

DATA ACCESSIBILITY

Model code and all data used in this study available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.2d0g778> (Girard, Shea, & Fisher, 2018).

All results in this article can be recreated using the code and data available within Dryad. In addition, the high-resolution images of corals used in this study can be found on the Gulf of Mexico Research Initiative Information and Data Cooperative (GRIIDC) repository (<https://data.gulfresearchinitiative.org>). Images collected in: 2011: <https://doi.org/10.7266/n78913tc> (Fisher 2016a); 2012: <https://doi.org/10.7266/n7hq3wvd> (Fisher, 2016b), 2013: <https://doi.org/10.7266/n7d21vjq> (Fisher, 2016c); 2014: <https://doi.org/10.7266/n74j0c2m> (Baums & Fisher, 2016); 2015: <https://doi.org/10.7266/n7cf9nh9> (Fisher, 2017).

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REFERENCES

- Andrews, A. H., Cordes, E. E., Mahoney, M. M., Munk, K., Coale, K. H., Cailliet, G. M., & Heifetz, J. (2002). Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. *Hydrobiologia*, 471, 101–110. <https://doi.org/10.1023/A:1016501320206>
- Baillon, S., Hamel, J.-F., Wareham, V. E., & Mercier, A. (2012). Deep cold-water corals as nurseries for fish larvae. *Frontiers in Ecology and the Environment*, 10, 351–356. <https://doi.org/10.1890/120022>
- Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Baums, I., & Fisher, C. R. (2016). Nautilus NA043: Sample records of corals and mussels collected around Macondo, Gulf of Mexico - June 22–July 4, 2014. Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG). GRIIDC Data Repository. <https://doi.org/10.7266/n74j0c2m>
- Bavestrello, G., Cerrano, C., Zanzi, D., & Cattaneo-Vietti, R. (1997). Damage by fishing activities to the Gorgonian coral *Paramuricea clavata* in the Ligurian Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 7, 253–262. [https://doi.org/10.1002/\(ISSN\)1099-0755](https://doi.org/10.1002/(ISSN)1099-0755)
- Buhl-Mortensen, L. (2004). Symbiosis in deep-water corals. *Symbiosis*, 37, 33–61.
- Buhl-Mortensen, L., & Mortensen, P. B. (2004). Crustaceans associated with the deep-water gorgonian corals *Paragorgia arborea* (L., 1758) and *Primnoa resedaeformis* (Gunn., 1763). *Journal of Natural History*, 38, 1233–1247. <https://doi.org/10.1080/0022293031000155205>
- Buhl-Mortensen, L., & Mortensen, P. B. (2005). Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In A. Freiwald & J.M. Roberts (Eds.), *Cold-water corals and ecosystems* (pp. 849–879). Berlin: Springer. <https://doi.org/10.1007/3-540-27673-4>
- Buhl-Mortensen, L., Vanreusel, A., Gooday, A.J., Levin, L.a., Priede, I.G., Buhl-Mortensen, P., ... Raes, M. (2010). Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology*, 31, 21–50. <https://doi.org/10.1111/j.1439-0485.2010.00359.x>
- Camilli, R., Reddy, C. M., Yoerger, D. R., Van Mooy, B. A. S., Jakuba, M. V., Kinsey, J. C., ... Maloney, J. V. (2010). Tracking hydrocarbon plume transport and biodegradation at Deepwater Horizon. *Science*, 330, 201–204. <https://doi.org/10.1126/science.1195223>
- Caswell, H. (2001). *Matrix population models: Construction, analysis, and interpretation*. Sunderland, MA: Sinauer Associates.
- Cathalot, C., Van Oevelen, D., Cox, T. J. S., Kutti, T., Lavaleye, M., Duineveld, G., & Meysman, F. J. R. (2015). Cold-water coral reefs and adjacent sponge grounds: Hotspots of benthic respiration and organic carbon cycling in the deep sea. *Frontiers in Marine Science*, 2, 37.
- Cerrano, C., Arillo, A., Azzini, F., Calcinai, B., Castellano, L., Muti, C., ... Bavestrello, G. (2005). Gorgonian population recovery after a mass mortality event. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15, 147–157. [https://doi.org/10.1002/\(ISSN\)1099-0755](https://doi.org/10.1002/(ISSN)1099-0755)
- Clark, M. R., & Koslow, J. A. (2008). Impacts of fisheries on seamounts. In T. J. Pitcher, T. Morato, P. J. B. Hart, M. R. Clark, N. Haggan, & R. S. Santos (Eds.), *Seamounts: Ecology, fisheries & conservation* (pp. 413–441). Oxford, UK: John Wiley & Sons.
- Clark, M. R., Rowden, A. A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K. I., ... Hall-Spencer, J. M. (2010). The ecology of seamounts: Structure, function, and human impacts. *Annual Review of Marine Science*, 2, 253–278. <https://doi.org/10.1146/annurev-marine-120308-081109>
- Cordes, E. E., Jones, D. O. B., Schlacher, T. A., Amon, D. J., Bernardino, A. F., Brooke, S., ... Witte, U. (2016). Environmental impacts of the

- deep-water oil and gas industry: A review to guide management strategies. *Frontiers in Environmental Science*, 4, 1–26
- DeLeo, D. M., Ruiz-Ramos, D. V., Baums, I. B., & Cordes, E. E. (2015). Response of deep-water corals to oil and chemical dispersant exposure. *Deep Sea Research Part II: Topical Studies in Oceanography*, 129, 137–147.
- Doughty, C. L., Quattrini, A. M., & Cordes, E. E. (2014). Insights into the population dynamics of the deep-sea coral genus *Paramuricea* in the Gulf of Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography*, 99, 71–82. <https://doi.org/10.1016/j.dsr2.2013.05.023>
- Du Preez, C., & Tunnicliffe, V. (2011). Shortspine thornyhead and rockfish (Scorpaenidae) distribution in response to substratum, biogenic structures and trawling. *Marine Ecology Progress Series*, 425, 217–231. <https://doi.org/10.3354/meps09005>
- Etnoyer, P., & Warrenchuk, J. (2007). A catshark nursery in a deep gorgonian field in the Mississippi Canyon, Gulf of Mexico. *Bulletin of Marine Science*, 81, 553–559.
- Fisher, C. R. (2016a). Coral image dataset for footprint of Deepwater Horizon blowout impact to deep-water coral communities, Gulf of Mexico, October 2011. Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG). GRIIDC data repository. <https://doi.org/10.7266/n78913tc>
- Fisher, C. R. (2016b). Coral images from the northern Gulf of Mexico, November 22–25 2012. Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG). GRIIDC Data Repository. <https://doi.org/10.7266/N7HQ3WVD>
- Fisher, C. R. (2016c). Nautilus NA028: ROV Cruise report – Sample records of corals, mussels and sediments collected around Macondo, Gulf of Mexico - June 21–July 5, 2013. Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG). GRIIDC Data Repository. <https://doi.org/10.7266/n7d21vjq>
- Fisher, C. R. (2017). Coral images around Macondo, Gulf of Mexico, Nautilus NA057 and NA058, April 22–May 11, 2015. Ecosystem impacts of oil and gas inputs to the Gulf-2 (ECOGIG-2). <https://doi.org/10.7266/N7CF9NH9>
- Fisher, C. R., Hsing, P.-Y., Kaiser, C. L., Yoerger, D. R., Roberts, H. H., Shedd, W. W., ... Brooks, J. M. (2014). Footprint of Deepwater Horizon blowout impact to deep-water coral communities. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 11744–11749. <https://doi.org/10.1073/pnas.1403492111>
- Frometa, J., DeLorenzo, M. E., Pisarski, E. C., & Etnoyer, P. J. (2017). Toxicity of oil and dispersant on the deep water gorgonian octocoral *Swiftia exserta*, with implications for the effects of the Deepwater Horizon oil spill. *Marine Pollution Bulletin*, 122, 91–99. <https://doi.org/10.1016/j.marpolbul.2017.06.009>
- Girard, F., Fu, B., & Fisher, C. R. (2016). Mutualistic symbiosis with ophiuroids limited the impact of the Deepwater Horizon oil spill on deep-sea octocorals. *Marine Ecology Progress Series*, 549, 89–98. <https://doi.org/10.3354/meps11697>
- Girard, F., Shea, K., & Fisher, C. R. (2018). Data from: Projecting the recovery of a long-lived deep-sea coral species after the Deepwater Horizon oil spill using state-structured models. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.2d0g778>
- Grasshoff, M. (1977). Die Gorgonarien des östlichen Nordatlantik und des Mittelmeeres III. Die Familie Paramuriceidae (Cnidaria, Anthozoa). *Meteor Forschungsergeb-Ergebnisse*, 27, 5–76.
- Hall-Spencer, J., Allain, V., & Fosså, J. H. (2002). Trawling damage to Northeast Atlantic ancient coral reefs. *Proceedings of the Royal Society B*, 269, 507–511. <https://doi.org/10.1098/rspb.2001.1910>
- Henry, L.-A., & Hart, M. (2005). Regeneration from injury and resource allocation in sponges and corals – A review. *International Review of Hydrobiology*, 90, 125–158. [https://doi.org/10.1002/\(ISSN\)1522-2632](https://doi.org/10.1002/(ISSN)1522-2632)
- Hsing, P.-Y., Fu, B., Larcum, E. A., Berlet, S. P., Shank, T. M., Govindarajan, A. F., ... Fisher, C. R. (2013). Evidence of lasting impact of the Deepwater Horizon oil spill on a deep Gulf of Mexico coral community. *Elementa: Science of the Anthropocene*, 1, 000012.
- Huvenne, V. A. I., Bett, B. J., Masson, D. G., Le Bas, T. P., & Wheeler, A. J. (2016). Effectiveness of a deep-sea cold-water coral marine protected area, following eight years of fisheries closure. *Biological Conservation*, 200, 60–69. <https://doi.org/10.1016/j.biocon.2016.05.030>
- Incardona, J. P., Gardner, L. D., Linbo, T. L., Brown, T. L., Esbaugh, A. J., Mager, E. M., ... Scholz, N. L. (2014). Deepwater Horizon crude oil impacts the developing hearts of large predatory pelagic fish. *Proceedings of the National Academy of Sciences of the United States of America*, 111, E1510–E1518. <https://doi.org/10.1073/pnas.1320950111>
- Koslow, J. A., Gowlett-Holmes, K., Lowry, J. K., O'Hara, T., Poore, G. C. B., & Williams, A. (2001). Seamount benthic macrofauna off southern Tasmania: Community structure and impacts of trawling. *Marine Ecology Progress Series*, 213, 111–125. <https://doi.org/10.3354/meps213111>
- Lasker, H. R. (1990). Clonal propagation and population dynamics of a gorgonian coral. *Ecology*, 71, 1578–1589. <https://doi.org/10.2307/1938293>
- Linares, C., Coma, R., Diaz, D., Zabala, M., Hereu, B., & Dantart, L. (2005). Immediate and delayed effects of a mass mortality event on gorgonian population dynamics and benthic community structure in the NW Mediterranean Sea. *Marine Ecology Progress Series*, 305, 127–137. <https://doi.org/10.3354/meps305127>
- Linares, C., Coma, R., Garrabou, J., Díaz, D., & Zabala, M. (2008). Size distribution, density and disturbance in two Mediterranean gorgonians: *Paramuricea clavata* and *Eunicella singularis*. *Journal of Applied Ecology*, 45, 688–699. <https://doi.org/10.1111/j.1365-2664.2007.01419.x>
- Lirman, D. (2000). Lesion regeneration in the branching coral *Acropora palmata*: Effects of colonization, colony size, lesion size, and lesion shape. *Marine Ecology Progress Series*, 197, 209–215. <https://doi.org/10.3354/meps197209>
- McNutt, M., Camilli, R., Guthrie, G., Hsieh, P., Labson, V., Lehr, B., ... Sogge, M. K. (2011). Assessment of flow rate estimates for the Deepwater Horizon/macondo well oil spill (pp. 1–22). Washington, DC, USA.
- Meesters, E. H., Noordeloos, M., & Bak, R. P. M. (1994). Damage and regeneration links to coral growth in the reef-building coral *Montastrea annularis*. *Marine Ecology Progress Series*, 112, 119–128. <https://doi.org/10.3354/meps112119>
- Meesters, E. H., Pauchli, W., & Bak, R. P. M. (1997). Predicting regeneration of physical damage on a reef-building coral by regeneration capacity and lesion shape. *Marine Ecology Progress Series*, 146, 91–99. <https://doi.org/10.3354/meps146091>
- Meesters, E. H., Wesseling, I., & Bak, R. P. M. (1996). Partial mortality in three species of reef-building corals and the relation with colony morphology. *Bulletin of Marine Science*, 58, 838–852.
- Mitra, S., Kimmel, D. G., Snyder, J., Scalise, K., McLaughon, B. D., Roman, M. R., ... Campbell, P. L. (2012). Macondo-1 well oil-derived polycyclic aromatic hydrocarbons in mesozooplankton from the northern Gulf of Mexico. *Geophysical Research Letters*, 39, 1–7.
- Oevelen, D. V., Duineveld, G., Lavaleye, M., Mienis, F., Soetaert, K., & Heip, C. H. R. (2009). The cold-water coral community as hotspot of carbon cycling on continental margins: A food-web analysis from Rockall Bank (northeast Atlantic). *Limnology and Oceanography*, 54, 1829–1844. <https://doi.org/10.4319/lo.2009.54.6.1829>
- Oren, U., Benayahu, Y., Lubinevsky, H., & Loya, Y. (2001). Colony integration during regeneration in the stony coral *Favia favaus*. *Ecology*, 82, 802–813. [https://doi.org/10.1890/0012-9658\(2001\)082\[0802:CIDRIT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0802:CIDRIT]2.0.CO;2)
- Passow, U. (2014). Formation of rapidly-sinking, oil-associated marine snow. *Deep Sea Research Part II: Topical Studies in Oceanography*, 129, 232–240.

- Passow, U., Ziervogel, K., Asper, V., & Diercks, A. (2012). Marine snow formation in the aftermath of the Deepwater Horizon oil spill in the Gulf of Mexico. *Environmental Research Letters*, 7, 035301 <https://doi.org/10.1088/1748-9326/7/3/035301>
- Peterson, C. H., Anderson, S. S., Cherr, G. N., Ambrose, R. F., Anghera, S., Bay, S., ... Adams, E. E. (2012). A tale of two spills: Novel science and policy implications of an emerging new oil spill model. *BioScience*, 62, 461–469. <https://doi.org/10.1525/bio.2012.62.5.7>
- Prouty, N. G., Fisher, C. R., Demopoulos, A. W. J., & Druffel, E. R. M. (2014). Growth rates and ages of deep-sea corals impacted by the Deepwater Horizon oil spill. *Deep Sea Research Part II: Topical Studies in Oceanography*, 129, 196–212.
- R Core Team. (2014). *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Roark, E. B., Guilderson, T. P., Dunbar, R. B., Fallon, S. J., & Mucciarone, D. A. (2009). Extreme longevity in proteinaceous deep-sea corals. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 5204–5208. <https://doi.org/10.1073/pnas.0810875106>
- Roberts, J. M., Wheeler, A. J., & Freiwald, A. (2006). Reefs of the deep: The biology and geology of cold-water coral ecosystems. *Science*, 312, 543–547. <https://doi.org/10.1126/science.1119861>
- Sánchez, J. A., & Lasker, H. R. (2003). Patterns of morphological integration in marine modular organisms: Supra-module organization in branching octocoral colonies. *Proceedings of the Royal Society B*, 270, 2039–2044. <https://doi.org/10.1098/rspb.2003.2471>
- Shea, K., & Kelly, D. (1998). Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications*, 8, 824–832. [https://doi.org/10.1890/1051-0761\(1998\)008\[0824:EBAIWM\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)008[0824:EBAIWM]2.0.CO;2)
- Stubben, C. J., & Milligan, B. G. (2007). Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, 22, 1–23.
- Van Dover, C. L. (2007). The biological environment of polymetallic sulphides deposits, the potential impact of exploration and mining on this environment, and data required to establish environmental baselines in exploration areas. Proceedings of the International Seabed Authority's Workshop, pp. 169–183.
- Verrill, A. E. (1894). Descriptions of new species of starfishes and ophiurans, with a revision of certain species formerly described; mostly from the collections made by the United States Commission of Fish and Fisheries. *Proceedings of the United States National Museum*, 1000, 245–297.
- Watling, L., France, S.C., Pante, E., & Simpson, A. (2011). Biology of deep-water octocorals. In M. Lesser (Ed.), *Advances in Marine Biology*, 60, pp. 42–122. Oxford UK:Elsevier
- White, H. K., Hsing, P. Y., Cho, W., Shank, T. M., Cordes, E. E., Quattrini, A. M., ... Fisher, C. R. (2012). Impact of the Deepwater Horizon oil spill on a deep-water coral community in the Gulf of Mexico. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 20303–20308. <https://doi.org/10.1073/pnas.1118029109>
- White, H. K., Lyons, S. L., Harrison, S. J., Findley, D. M., Liu, Y., & Kujawinski, E. B. (2014). Long-term persistence of dispersants following the Deepwater Horizon oil spill. *Environmental Science & Technology Letters*, 1, 295–299. <https://doi.org/10.1021/ez500168r>

SUPPORTING INFORMATION

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